

BULLETIN
of **CARNEGIE MUSEUM OF NATURAL HISTORY**

**THE APPENDICULAR MYOLOGY AND PHYLOGENETIC
RELATIONSHIPS OF THE PLOCEIDAE AND
ESTRILDIDAE (AVES: PASSERIFORMES)**

GREGORY DEAN BENTZ

*Mount Vernon College,
Washington, D.C. 20007*

BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 15, pages 1-25, figures 1-5, tables 1-2

Issued 15 June 1979

Price: \$2.00 a copy

Craig C. Black, *Director*

Editorial Staff: Hugh H. Genoways, *Editor*; Duane A. Schlitter,
Associate Editor; Stephen L. Williams, *Associate Editor*;
Barbara Farkas, *Technical Assistant*.

© 1979 by the Trustees of Carnegie Institute, all rights reserved.

CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

CONTENTS

Abstract	5
Introduction	5
Methods and Materials	7
Muscles of the Forelimb	8
<i>M. latissimus dorsi</i>	8
<i>M. coracobrachialis cranialis</i>	10
<i>M. tensor propatagialis</i>	10
<i>M. deltoideus minor</i>	11
<i>M. pronator profundus</i>	11
Muscles of the Hindlimb	13
<i>M. iliotibialis lateralis</i>	13
<i>M. ilioprochantericus medius</i>	15
<i>M. obturatorius lateralis</i>	15
<i>M. gastrocnemius</i>	16
<i>M. plantaris</i>	16
<i>M. flexor digitorum longus</i>	17
<i>M. extensor hallucis longus</i>	18
Discussion	18
Cluster 1	20
Cluster 2	20
Cluster 3	20
Cluster 4	20
Cluster 5	20
Cluster 6	20
Autapomorphic Characters	21
Conclusions and Taxonomic Recommendations	22
Acknowledgments	24
Literature Cited	24



ABSTRACT

The phylogenetic relationships of the Old World passerine families Ploceidae and Estrildidae are analyzed mainly on the basis of the structure of the forelimb and hindlimb muscles. Monophyly of the assemblage is hypothesized on the basis of common possession of a conical bill adapted to granivory, on biochemical affinities, and in pterylographic similarities previously reported. The present study provided no myological synapomorphies to cluster the entire group in support of this hypothesis. Myological characters provide synapomorphies for all but the first branching point of a cladogram, and autapomorphies

for most taxa. Analysis is at the subfamily level. The Passerinae are the most primitive group myologically, and presumably the sister group of the remainder of the assemblage. The Estrildidae are more highly derived than are the Ploceidae. The Viduinae are included among the Estrildidae rather than the Ploceidae. Problems of classification are reviewed and a classification reflecting current understanding is presented. The family Ploceidae includes the subfamilies Passerinae, Ploceinae and Bubalornithinae. The Estrildidae includes the Poephilinae, Viduinae, Lonchurinae, and Estrildinae.

INTRODUCTION

The Old World finches, as the term is used herein, form a group of approximately 46 genera and 268 species (Moreau and Greenway, 1962; Mayr et al., 1968) in the families Ploceidae and Estrildidae. Excluding introductions, they are Old World in distribution and are especially numerous in Africa. The bill is short, and typically rather thick and sharply pointed to massive in adaptation to seed cracking. There are ten primaries. One subfamily, the Viduinae (10 species), is entirely parasitic, often laying their eggs in the nests of estrildids.

The purpose of this study is to elucidate the phylogenetic relationships of the Old World finch assemblage by constructing a cladogram based on a survey of the appendicular muscles. This will make it possible to suggest answers to several related taxonomic questions, some of which were summarized by Sibley (1970).

Historically there has been discussion over whether the Ploceinae and Estrildinae should be included in one family or two. Are the Widow Birds (*Vidua*) more closely related to the ploceines, the estrildines, or to some other group? Is *Passer* more closely related to the ploceines, the estrildines, the fringillids, or some other group? Should a family Passeridae be recognized? What are the closest relatives of such genera as *Bubalornis*, *Philetairus*, *Plocepasser*, and *Sporopipes*? Finally, does the Old World finch assemblage constitute a monophyletic group, or is it polyphyletic?

The taxonomic history of this group is long and complicated and the following is only a brief summary; a thorough review was given by Sibley (1970). Some authors have used obsolete generic names. In those cases the current generic name as

it appears in the "Check-list of Birds of the World" is given in parentheses.

In the past the principal character used to distinguish the Ploceidae (including Estrildidae) from the Fringillidae was that in the former the tenth primary is present and usually relatively large on the dorsal side of the wing, whereas in the latter it is very small and concealed ventrally.

The first modern classification of the Old World finches ("Ploceidae") was given by Chapin (1917). Before that the family was divided into two subfamilies mainly on the length of the tenth primary—the Ploceinae with a tenth primary longer than the upper primary coverts and the Viduinae with a small and falcate tenth primary. Chapin believed that a better idea of relationships would result if attention was given to additional characters, such as song, plumage, nest construction, bill and foot form, egg color, and habits. One character, the mouth markings in estrildid nestlings, has been extremely useful, and Chapin described two types. The "domino" mouth has symmetrically arranged black spots on a pale palate, whereas the "horseshoe" type lacks spots on the palate but has one or two horseshoes or inverted U-shaped lines, a black line around the tongue, and two crescents beneath it. Chapin removed from the Estrildinae those forms whose nestlings lack such markings. Species with nestling mouth markings, even though they also have a long outer primary, were placed in the Estrildinae.

Chapin placed "*Textor*" (*Bubalornis*) and *Dinemellia* in a separate family, Textoridae (Bubalornithidae), based on characters of the skull and sternum. In *Bubalornis* the fenestrae associated with the orbital foramina differ in extent and number

from other ploceids, and have an obliquely ascending median bar that is lacking in the other genera examined. According to Chapin (1917), *Bubalornis* also differs from certain ploceids in the form of the sternal rostrum, which is less forked and more square in outline, and has a spina interna, as well as a spina externa. Both Chapin (1917) and Sushkin (1927) note the presence of a phalloid organ in *Bubalornis*, which I have also observed. Sushkin suggested that this structure served as an auxiliary copulatory organ.

Shelley (1905) placed all longtailed ploceids in a subfamily Viduinae to which the Bishop-Birds (*Euplectes*) were added. Reichenow (1914), however, included them all in his Spermestinae (+ Estrildinae) but did not so closely associate *Vidua* with *Coliuspasser* (*Euplectes*). Chapin (1917) placed *Vidua* in the Estrildinae and *Coliuspasser* in the Ploceinae. *Vidua* and three closely allied genera, *Tetraenura*, *Linura*, and *Steganura* (currently all considered *Vidua*; Mayr et al., 1968) have only the two median pairs of rectrices elongated, whereas in *Coliuspasser* all twelve are lengthened. Chapin attributed this to parallelism. The relationship between *Hypochera* (*Vidua*), *Vidua* (*sens. strict.*), and *Steganura* is further strengthened by a peculiar condition in the braincase; the skull has a large clear area in the frontal region, remaining throughout life, whereas *Coliuspasser* has normal skull ossification.

Sushkin (1927) divided the Ploceidae into six subfamilies—Bubalornithinae, Plocepasserinae, Ploceinae, Sporopipinae, Estrildinae, and Passerinae, creating the last subfamily by removing *Passer*, *Petronia*, and *Montifringilla* from the Fringillidae. He considered them ploceids because they share a characteristic relief of the horny palatal surface, molt the juvenile remiges and tail in the autumn, and build a domed nest with a side entrance. The unity of this group was supported by Bock and Morony (1978) on the basis of the preglossale, a unique skeletal element of the tongue.

Sushkin stated that *Bubalornis* and *Dinemellia* are closely allied, but that *Dinemellia* lacks some "primitive" features of *Bubalornis*, pointing more in the direction of the "advanced" Ploceidae. He used the terms "primitive" and "advanced" but provided no basis for their usage. Further, the group of *Plocepasser*, *Philetairus*, and *Pseudonigrita* fills the gap between the Bubalornithinae and the Passerinae to a great extent, which serves to make the separation of *Bubalornis* from the remainder of the group less meaningful. *Bubalornis*

and *Dinemellia*, then, constitute the Bubalornithinae. The Passerinae are a close-knit group that is nearer to the Ploceinae than to the Estrildinae. In some osteological respects the Passerinae are more "primitive" than either. In other respects, such as specialized feathers at the base of the bill, the Passerinae are more "advanced" than either the Ploceinae or Estrildinae. The connection to the Bubalornithinae is established via *Philetairus*, *Plocepasser*, and *Pseudonigrita* or the Plocepasserinae. On the basis of osteology, Sushkin stated that the Estrildinae are more advanced than the Ploceinae. *Vidua* and *Steganura* appear to be the least specialized of the Estrildinae and differ least from the Ploceinae. Sushkin stated that *Sporopipes* was halfway between the primitive Estrildinae and *Plocepasser*, or even *Bubalornis*, and separated it as a subfamily Sporopipinae.

The subfamily Estrildinae has often been divided into two groups whose relationship has frequently been debated. Chapin (1917) believed that the Viduinae and Estrildinae were very close because of the similar mouth markings of their young, and that these markings were not acquired independently. Beecher (1953) raised the group to the rank of family, Estrildidae. He believed that the Viduinae arose in Africa from the Ploceinae and only later became parasitic on the estrildids, which came to Africa from Australia. Delacour and Edmond-Blanc (1933–1934) revised *Euplectes* and *Vidua* and proposed that a separate subfamily, Viduinae, be recognized in the Ploceidae for the Widow Birds. Delacour (1943) revised the Estrildinae and concluded that their nearest relatives are the Viduinae, and that both groups evolved from the Sporopipinae. He suggested that the Ploceidae were closer to the Sturnidae than to the Fringillidae because of their nesting habits. Roberts (1947) divided the Ploceidae into eleven subfamilies. Neither Roberts' nor Delacour's work has been universally accepted as they represent the extremes of taxonomic philosophy—Roberts as a "splitter" and Delacour as a "lumper."

Tordoff (1954) transferred the Carduelinae from the Fringillidae to the Ploceidae, based primarily on the condition of the bony palate. Wolters (1949), Steiner (1954), and Mayr (1955) also transferred the Carduelinae to the Ploceidae; however, Bock (1960) disagreed. In an exhaustive analysis, he concluded that the palatine process had little value in showing relationships among passerine families.

Stallcup (1954) argued that in hindlimb myology

and serology the carduelines are most similar to the estrildines, and placed the two subfamilies in a family Carduelidae. Raikow (1978) included the Carduelinae in the Fringillidae based on the limb muscles.

Friedmann (1960) reviewed the literature on the parasitic weavers and on the basis of reflection globules, nestling behavior, and plumage, concluded that the Widow Birds were most closely related to the estrildines but were distinctive enough to be considered a subfamily Viduinae.

In the widely followed "Check-list of Birds of the World" (Moreau and Greenway, 1962; Mayr et al., 1968; Traylor, 1968), two families (Ploceidae, Estrildidae) were recognized. The Ploceidae were divided into the subfamilies Viduinae, Bubalornithinae, Passerinae, and Ploceinae. No subfamilies were recognized in the Estrildidae, but the genera

are arranged in three groups of undesigned taxonomic status—Estrildae, Poephilae, and Lonchuridae.

Sibley (1970) studied the egg-white proteins of passerine birds. He concluded that the ploceids and estrildids are related to one another more closely than either is to any other group, and recommended that they be placed in the same family. He also suggested that a family Passeridae be recognized until there is more information on *Passer*.

On the basis of pterylosis, Morlion (1966, 1979) found two groups, one consisting of Ploceinae, the other of Viduinae and Estrildinae (which were not separable). She concluded that recognition of two families could not be supported on the basis of pterylosis alone, but if the Ploceidae and Estrildidae were upheld for other reasons, the Viduinae clearly belonged to the Estrildidae, not to the Ploceidae.

METHODS AND MATERIALS

Variations in musculature were analyzed to determine ancestral and derived character states. Though logical and precise, this methodology does not provide automatic answers, and interpretive decisions are required in situations involving character conflicts. For example, an individual species of a traditional group may show an isolated ancestral character state. Precise application of cladistic methodology might prevent this species from being grouped with its presumed closest relatives because sister groups must share derived states that have presumably been acquired from a common ancestor. However, these isolated variations are explainable and what is achieved is a cladogram that represents the best fit with the data available. Character conflict is discussed in further detail in the discussion.

Hennig (1966), Kluge (1971), Maslin (1952), and Ross (1974) gave several methods for analyzing character states. The most important method for this study is the *outgroup comparison* between the group being analyzed and related groups. The outgroup comparison may be stated as follows: If a character varies within a group and one of the variants is also found in a closely related outside group, then the character state that occurs in both groups is primitive within the group being studied. It is supposed that the two groups arose by splitting from a common ancestor, and that the character states that both groups share are derived from that ancestor (Kluge, 1971:25–26; Ross, 1974:152–156).

Another method employed is the *ingroup correlation*. This states (Kluge, 1971:26) that a character state restricted to the group of organisms being studied, although only infrequently exhibited, is primitive when it occurs in those individuals that have the greatest number of primitive states as determined by other methods. The probability that a character state is primitive increases markedly with the increase in the number of primitive characters with which it is positively correlated. This method is

of limited use, however, because there is no way of knowing whether a character state is primitive or derived simply from its frequency of occurrence.

Wiley (1975:234) has stressed that the determination of ancestral and derived character states is ultimately a question of homologies and that such homologies are not empirical facts but hypotheses to be tested. Derived character states are hypothesized to have been acquired from the immediate ancestral species and to be absent in earlier common ancestors.

It is hypothesized herein that the Old World finches are a monophyletic group and that the finch-type bill and seed-eating habit arose only once, as explained below. The outgroups employed in this study are other birds in general and especially other groups of passerines. Much of the anatomical data on these groups has been summarized by George and Berger (1966). The New World nine-primaried oscines have been analyzed by Raikow (1978) and are also used for outgroup comparisons because their myology indicates a close relationship to the ploceids and estrildids.

The term "passerine" is an adjective referring to members of the order Passeriformes and is not to be confused with the subfamily Passerinae.

All of the hindlimb and forelimb muscles were dissected and described in *Ploceus cucullatus* and 47 additional forms. This species was chosen because of the number of specimens available and because *Ploceus* is the nominate genus of the Ploceidae. Of the 46 genera listed in the "Check-list of Birds of the World," 40 were available for this study. The species dissected are listed below. Dissection was aided by a stereomicroscope at magnifications of 6× to 25×. Visibility of small muscles and fiber arrangements was improved by an iodine stain (Bock and Shear, 1972). Only one specimen of each species was dissected, with the exception of *P. cucullatus* of which six specimens were ex-

amed. The range of myological variations among those six specimens was so minute that a single specimen of each additional species was considered adequate.

Species dissected (nomenclature of "Check-list of Birds of the World") were as follows:

Ploceidae

Viduinæ

Vidua paradisæa

Bubalornithinæ

Bubalornis albirostris

Dinemellia dinemelli

Passerinae

Plocepasser mahali

Pseudonigrita cabinisi

Philetairus socius

Passer domesticus

Petronia xanthocollis

Montifringilla nivalis

Sporopipes sp.

Ploceinae

Amblyospiza albifrons

Ploceus ocularis

Ploceus nigricollis

Ploceus cucullatus

Malimbus cassini

Quelea quelea

Foudia madagascariensis

Euplectes afer

Anomalospiza imberbis

Estrildidae

Estrildæ

Parnoptila woodhouseii

Nigrita canicapilla

Pytilia sp.

Mandingoa nitidula

Cryptospiza reichenovii

Pyrenestes sanguineus

Pyrenestes ostrinus

Spermophaga haematina

Spermophaga ruficapilla

Clytospiza monteiri

Hypargos niveoguttatus

Lagonosticta senegala

Uraeginthus ianthinogaster

Estrilda paludicola

Estrilda astrild astrild

Estrilda astrild angolensis

Amandava amandava

Ortygospiza atricollis

Poephilæ

Aegintha temporalis

Emblema guttata

Neochmia phaeton

Poephila guttata

Poephila acuticauda

Lonchuræ

Erythrura trichroa

Chloebia gouldiæ

Lonchura striata

Lonchura punctulata

Padda oryzivora

Amadina fasciata

The myological nomenclature used is that employed by Raikow (1976, 1977).

In the following section "Structure" describes the condition found in *P. cucullatus*. Variations in other species are included in "Comparisons," and comments on derived versus primitive character states appear under "Discussion."

Drawings were made with the aid of a camera lucida microscope attachment. Because the general pattern of musculature is similar to that in the New World nine-primaries oscines as described and illustrated by Raikow (1976, 1977), similar diagrams and descriptions of all muscles were not included here as this would be repetitious. Instead, the descriptions and illustrations in the present work show variations that are significant to this study.

MUSCLES OF THE FORELIMB

The following muscles are present in the forelimb of *Ploceus* but do not differ significantly from those of *Loxops virens* as described by Raikow (1976): M. rhomboideus superficialis; M. rhomboideus profundus; M. serratus profundus; M. serratus superficialis; M. scapulohumeralis cranialis; M. scapulohumeralis caudalis; M. subscapularis; M. subcoracoideus; M. pectoralis; M. supracoracoideus; M. coracobrachialis caudalis; M. sternocoracoideus; M. cucullaris capitis pars proptagialis; M. deltoideus major; M. biceps brachii; M. triceps brachii; M. expansor secundariorum; M. brachialis; M. pronator superficialis; M. flexor digitorum superficialis; M. flexor digitorum profundus; M. flexor carpi ulnaris; M. ulnometacarpalis ventralis; M. ex-

tensor metacarpi radialis; M. extensor metacarpi ulnaris; M. extensor digitorum communis; M. ectepicondyloulnaris; M. supinator; M. extensor longus digiti majoris; M. extensor longus alulae; M. ulnometacarpalis dorsalis; M. abductor alulae; M. adductor alulae; M. abductor digiti majoris; M. interosseus dorsalis; M. interosseus ventralis; M. flexor digiti minoris.

M. LATISSIMUS DORSI

Structure.—Pars cranialis arises by an aponeurosis from the neural spines of the last cervical and first dorsal vertebrae. The thin, strap-shaped, parallel-fibered belly passes laterally between the bellies of M. scapulothriceps and M. humerotriceps of

Table 1.—Major variations in forelimb myology of the *Ploceidae* and *Estrildidae*. *M. latissimus dorsi pars caudalis*: + = muscle present, - = muscle absent. *M. coracobrachialis cranialis*: + = present, - = absent. *M. tensor propatagialis pars brevis*: Type 1 = normal belly; Type 2 = elongated belly. *M. deltoideus minor*: Type 1 = normal condition; Type 2 = double-headed condition; Type 3 = expanded origin. *M. pronator profundus*: Type 1 = single belly; Type 2 = double belly.

Species	<i>M. latissimus dorsi pars caudalis</i>	<i>M. coracobrachialis cranialis</i>	<i>M. tensor propatagialis pars brevis</i>	<i>M. deltoideus minor</i>	<i>M. pronator profundus</i>
Family Ploceidae					
Subfamily Viduinae					
<i>Vidua paradisaea</i>	+	-	Type 1	Type 1	Type 1
Subfamily Bubalornithinae					
<i>Bubalornis albirostris</i>	+	+	Type 1	Type 1	Type 1
<i>Dinemella dinemelli</i>	+	+	Type 1	Type 1	Type 1
Subfamily Passerinae					
<i>Plocepasser mahali</i>	+	-	Type 1	Type 1	Type 1
<i>Pseudonigrita cabanisi</i>	+	-	Type 1	Type 1	Type 1
<i>Philetairus socius</i>	+	-	Type 1	Type 1	Type 1
<i>Passer domesticus</i>	-	-	Type 1	Type 3	Type 1
<i>Petronia xanthocollis</i>	-	-	Type 1	Type 1	Type 1
<i>Montifringilla nivalis</i>	-	-	Type 1	Type 3	Type 1
<i>Sporopipes</i> sp.	+	-	Type 1	Type 1	Type 1
Subfamily Ploceinae					
<i>Amblyospiza albifrons</i>	+	-	Type 1	Type 1	Type 1
<i>Ploceus ocularis</i>	+	-	Type 1	Type 1	Type 1
<i>Ploceus nigricollis</i>	+	-	Type 1	Type 1	Type 1
<i>Ploceus cucullatus</i>	+	-	Type 1	Type 1	Type 1
<i>Malimbus cassini</i>	+	-	Type 1	Type 1	Type 1
<i>Quelea quelea</i>	+	-	Type 1	Type 1	Type 1
<i>Foudia madagascariensis</i>	+	-	Type 1	Type 2	Type 1
<i>Euplectes afer</i>	+	-	Type 1	Type 1	Type 1
<i>Anomalospiza imberbis</i>	+	-	Type 1	Type 1	Type 1
Family Estrildidae					
Tribe Estrildae					
<i>Parmoptila woodhouseii</i>	+	-	Type 1	Type 1	Type 1
<i>Nigrita canicapilla</i>	+	-	Type 1	Type 1	Type 1
<i>Pytilia</i> sp.	-	-	Type 1	Type 1	Type 1
<i>Mandingoa nitidula</i>	-	-	Type 1	Type 1	Type 2
<i>Cryptospiza reichenovii</i>	-	-	Type 1	Type 1	Type 1
<i>Pyrenestes sanguineus</i>	-	-	Type 1	Type 1	Type 2
<i>Pyrenestes ostrinus</i>	-	-	Type 1	Type 1	Type 2
<i>Spermophaga haematina</i>	+	-	Type 1	Type 1	Type 1
<i>Spermophaga ruficapilla</i>	+	-	Type 1	Type 1	Type 1
<i>Clytospiza monteiri</i>	-	-	Type 1	Type 1	Type 1
<i>Hypargos niveoguttatus</i>	+	-	Type 1	Type 1	Type 2
<i>Lagonosticta senegala</i>	+	-	Type 1	Type 2	Type 2
<i>Uraeginthus ianthinogaster</i>	-	-	Type 1	Type 1	Type 1
<i>Estrilda paludicola</i>	-	-	Type 1	Type 1	Type 1
<i>Estrilda astrild astrild</i>	-	-	Type 1	Type 1	Type 1
<i>Estrilda astrild angolensis</i>	+	-	Type 1	Type 1	Type 1
<i>Amandava amandava</i>	-	-	Type 1	Type 1	Type 1
<i>Ortygospiza atricollis</i>	-	-	Type 1	Type 1	Type 2
Tribe Poephilae					
<i>Aegintha temporalis</i>	+	-	Type 1	Type 1	Type 2
<i>Emblema guttata</i>	+	-	Type 1	Type 1	Type 1
<i>Neochmia phaeton</i>	+	-	Type 1	Type 1	Type 2
<i>Poephila guttata</i>	+	-	Type 1	Type 1	Type 1
<i>Poephila acuticauda</i>	+	-	Type 1	Type 1	Type 2

Table 1.—Continued.

Species	M. latissimus dorsi pars caudalis	M. coracobrachialis cranialis	M. tensor propatagialis pars brevis	M. deltoideus minor	M. pronator profundus
Tribe Lonchurae					
<i>Erythrura trichroa</i>	+	—	Type 1	Type 1	Type 1
<i>Chloebia gouldiae</i>	+	—	Type 2	Type 1	Type 1
<i>Lonchura striata</i>	+	—	Type 2	Type 1	Type 1
<i>Lonchura punctulata</i>	+	—	Type 2	Type 1	Type 1
<i>Padda oryzivora</i>	+	—	Type 1	Type 1	Type 1
<i>Amadina fasciata</i>	+	—	Type 2	Type 1	Type 1

M. triceps brachii to a fleshy insertion on the dorsal surface of the humerus about 3 mm from the proximal end of the bone.

Pars caudalis arises by an aponeurosis from the third and fourth dorsal vertebrae. The thin, parallel-fibered belly passes laterally superficial to *M. rhomboideus profundus*, tapers to a thin tendon, and inserts on the caudodorsal surface of the head of the humerus. The insertion is deep and cranial to the insertion of pars cranialis.

Comparison.—Pars caudalis was present in all Ploceinae, Bubalornithinae, Lonchurae, Poephila, and *Vidua*. It was absent in many of the Estrildae and in three species of Passerinae (Table 1).

Discussion.—Because pars caudalis is present in many passerine and non-passerine birds (George and Berger, 1966:288–292; Raikow, 1978) its presence here is clearly primitive and its absence derived.

M. CORACOBRACHIALIS CRANIALIS

Structure.—This muscle is absent in *Ploceus*, and the following description is based on *Bubalornis albirostris*. This parallel-fibered muscle arises by tendinous fibers from the lateral surface of the head of the coracoid. The fibers of the muscle are embedded in thick fascia and pass distally to insert fleshy on the ventral surface of the head of the humerus, halfway between the coracohumeral ligament and the belly of *M. deltoideus minor*.

Comparison.—This muscle is present only in *Bubalornis* and *Dinemellia*. In all other forms examined it is represented by a ligamentous band.

Discussion.—George and Berger (1966:313) stated that this muscle is absent in *Agelaius phoeniceus* because no muscle fibers are visible. *Ploceus cucullatus* exhibits a similar condition except that a very few muscle fibers appear to be present. Because this muscle is present in many groups of birds

its presence in *Bubalornis* and *Dinemellia* probably represents an ancestral state. Absence of the muscle represents a loss and is therefore derived.

M. TENSOR PROPATAGIALIS

Structure.—*M. tensor propatagialis pars longa* is a small parallel-fibered muscle about 9 mm long and 3 mm wide. It arises by both fleshy fibers and an aponeurosis from the apex of the clavicle immediately proximal to the origin of *M. tensor propatagialis pars brevis*. The belly of *M. tensor propatagialis pars longa* ends on a thin tendon that passes distally in the cranial edge of the propatagium and is joined by the tendon of *M. cucullaris capitis pars propatagialis*. The tendon then passes superficial to the tendon of insertion of *M. extensor metacarpi radialis* to insert on the distal end of the radius and on the palmar surface of the os radiale. The tendon also fuses with thick fascia around the wrist and hand.

A much larger head than *M. tensor propatagialis pars longa*, the pars brevis has both a fleshy and tendinous origin from the apex of the clavicle. The 13 mm spindle-shaped belly tapers to a strong 9 mm tendon that is joined by the pars propatagialis brevis of *M. pectoralis* and fuses with the belly of *M. extensor metacarpi radialis*. The tendon of *M. tensor propatagialis pars brevis* then passes proximad along the dorsal surface of the belly of *M. extensor metacarpi radialis* to insert on the ectepicondylar process of the humerus.

Comparison.—In many of the Lonchurae the belly of pars brevis is elongated to within 1 mm of the insertion on *M. extensor metacarpi radialis* (Fig. 1 and Table 1).

Discussion.—According to George and Berger (1966:320) there has been emphasis on the taxonomic value of the pattern formed by the tendon of insertion of pars brevis. The condition in the Lon-

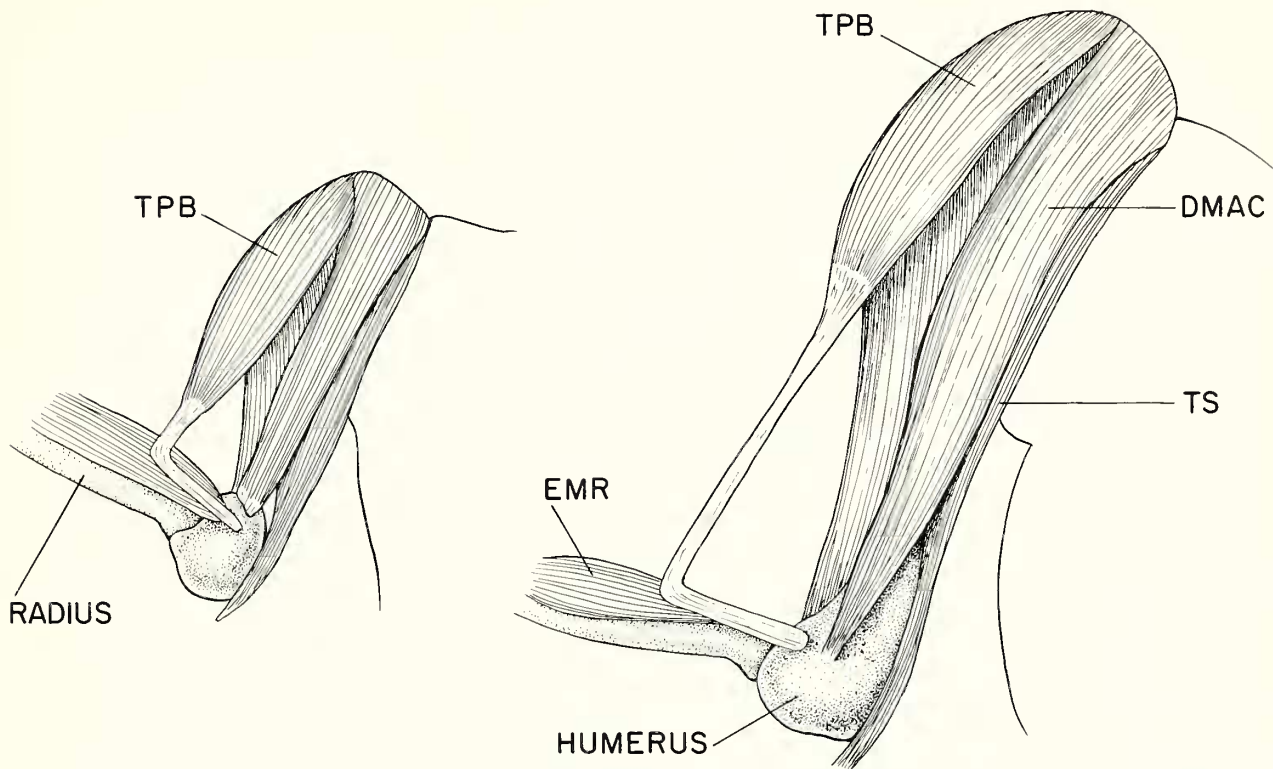


Fig. 1.—Dorsal view of the left shoulder. Left: derived condition of *M. tensor proptagialis pars brevis* (TPB) in *Lonchura punctulata*. Right: ancestral condition of the same muscle in *Ploceus cucullatus*. Abbreviations: DMAC, *M. deltoideus major caudalis*; TS, *M. scapulotriceps*; EMR, *M. extensor metacarpi radialis*.

churae closely resembles the condition characteristic of some swifts, hummingbirds, and pigeons. However most birds, including the New World nine-primaried oscines (Raikow, 1978), show a condition similar to *Ploceus*. By outgroup comparison then the described condition is primitive and the elongated condition is derived.

M. DELTOIDEUS MINOR

Structure.—This small flat band of fleshy, nearly parallel fibers is about 7 mm long and 0.5 mm wide. It arises from the ventral and lateral edges of the acromion process of the scapula. The belly passes laterally and cranially superficial to the tendon of insertion of *M. supracoracoideus* and inserts on the craniodorsal surface of the deltoid crest just distal to the insertion of *M. supracoracoideus*.

Comparison.—Most ploceids and estrildids exhibit the condition described above. However, two distinct variations occur. In *Foudia* and *Lagonosticta* this muscle arises by two independent heads that fuse prior to insertion. In *Passer* and *Montifringilla* the origin is from the scapula, the scapulocoracoidal ligament and the head of the coracoid.

Raikow (1978) found this latter condition in certain genera of the New World nine-primaried oscines.

Discussion.—George and Berger (1966:236) state: “*M. deltoideus minor* typically has a single head . . . which has been found in most birds.” On the basis of outgroup comparison then, the condition described for *Ploceus* represents an ancestral state and the two variations described above are derived character states.

M. PRONATOR PROFUNDUS

Structure.—This muscle arises fleshy from the humeroulnar pulley and by means of a short tendon from the distal end of the humerus (between the origins of *M. pronator superficialis* and *M. flexor digitorum superficialis*). The fan-shaped belly passes distally to insert on the caudal surface of the proximal one-third of the radius.

Comparison.—In several Estrildidae there are two distinct heads (Table 1). The muscle originates as described above, but at its midpoint the belly divides into two portions. The proximal belly inserts fleshy onto the ventral surface of the radius. The distal belly tapers to a 5 mm wide aponeurosis

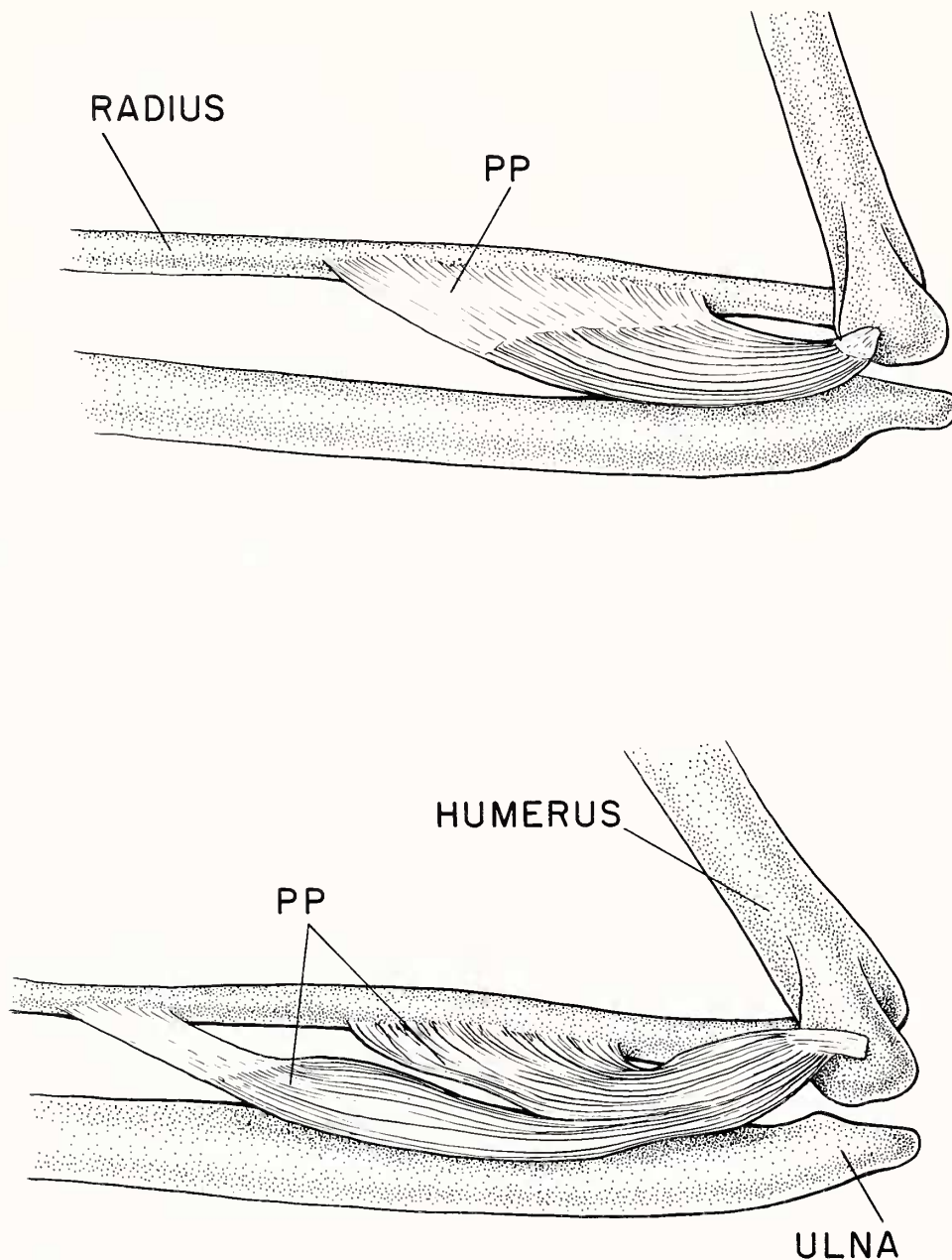


Fig. 2.—A deep muscle of the forearm, *M. pronator profundus*, PP. Above: ancestral condition in *Ploceus cucullatus*. Below: derived condition in *Hypargos niveoguttatus*.

and inserts on the radius approximately 5 mm distal to the insertion of the proximal belly (Fig. 2). Berger (1968) described a similar condition in *Dendroica kirtlandii*. Raikow (1978) also found two heads in some of the New World nine-primaried oscines.

Discussion.—The condition of this muscle in *Ploceus* is as it is in most birds (George and Berger, 1966:346). It therefore represents an ancestral character state. The two-headed condition is a derived state within this group, by virtue of the outgroup comparison.

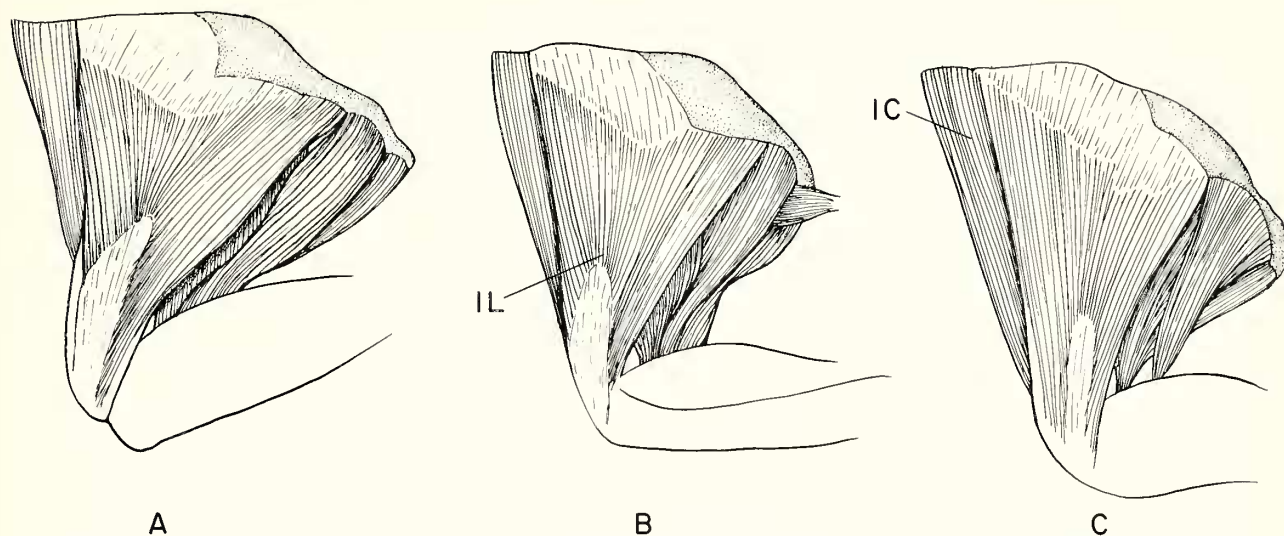


Fig. 3.—Lateral view of thigh musculature showing variation in the origin of the postacetabular portion of *M. iliobtibialis lateralis* (IL). A, condition as it exists in *Ploceus cucullatus*; B, *Cryptospiza reichenovii*; C, *Plocepasser mahali*. Abbreviation: IC, *M. iliobtibialis cranialis*.

MUSCLES OF THE HINDLIMB

The following muscles are present in the hindlimb of *Ploceus* but do not differ significantly from those of *Loxops virens* as described by Raikow (1977): *M. iliobtibialis cranialis*; *M. iliobtibialis lateralis*; *M. iliobtibialis caudalis*; *M. iliobtibialis cranialis*; *M. femorotibialis internus*; *M. iliofibularis*; *M. flexor cruris lateralis*; *M. caudoiliofemoralis pars caudofemoralis*; *M. flexor cruris medialis*; *M. puboischiofemoralis*; *M. ischiofemoralis*; *M. obturatorius medialis*; *M. iliofemoralis internus*; *M. peroneus longus*; *M. peroneus brevis*; *M. tibialis cranialis*; *M. extensor digitorum longus*; *M. flexor perforans et perforatus digiti III*; *M. flexor perforans et perforatus digiti II*; *M. flexor perforatus digiti II*; *M. flexor perforatus digiti IV*; *M. flexor perforatus digiti III*; *M. flexor hallucis longus*; *M. flexor hallucis brevis*; *M. lumbricalis*.

M. ILIOTIBIALIS LATERALIS

Structure.—This broad, triangular muscle arises by a large aponeurosis from the dorsal (anterior) iliac crest and most of the dorsolateral (posterior) iliac crest. The origin is fleshy for its caudal 2 to 3 mm. Cranially this aponeurotic origin obscures *M. iliobtibialis cranialis* and *M. iliobtibialis caudalis*. Indeed the entire muscle conceals most of

the deeper muscles of the lateral aspect of the thigh. The distal half of this muscle consists of three distinct parts—the cranial and caudal edges are fleshy, whereas the central part is aponeurotic. The fleshy cranial and caudal parts become aponeurotic just proximal to the knee. The common aponeurosis of these three distal parts forms the outer or cranial layer of the patellar ligament. The insertion is tendinous on a line joining the cnemial crests of the tibiotarsus.

Comparison.—In all forms studied this muscle consists of well-developed preacetabular, acetabular, and postacetabular portions. There are, however, two variations from the condition described above (Fig. 3). In *Plocepasser* and *Montifringilla* the origin of the postacetabular portion is entirely aponeurotic. In *Sporopipes*, *Pseudonigrita* and in most Estrildidae examined the postacetabular portion was entirely fleshy in origin. The estrildid exceptions to this were *Aegintha* and *Lagonosticta*, in which approximately half of the postacetabular portion was fleshy, and *Spermophaga ruficapilla*, *Parmoptila*, *Pyrenestes sanguineus*, and *Padda*, which were as described.

Discussion.—By outgroup comparison with most other birds (George and Berger, 1966) the aponeu-

Table 2.—Major variations in the hindlimb myology of the Ploceidae and Estrildidae. *M. gastrocnemius pars interna*: Type 1 = anterior head present, including patellar band; Type 2 = anterior head present but lacking patellar band; Type 3 = anterior head absent. Patellar band: size expressed as percentage of length of patellar ligament covered by muscular origin. *M. obturatorius lateralis pars dorsalis*: — = dorsal head absent; small, medium, and large size as defined in text. *M. plantaris*: + = present, — = absent. *M. iliiochantericus medius*: + = present, — = absent. *M. iliotibialis lateralis*: Type 1 = postacetabular portion entirely aponeurotic; Type 2 = condition as described in text for Ploceus; Type 3 = postacetabular portion entirely fleshy. *M. flexor digitorum longus*: variations in insertions of accessory vincula as described in text.

Species	<i>M. gastrocnemius pars interna</i>	Patellar band	<i>M. obturatorius lateralis pars dorsalis</i>	<i>M. plantaris</i>	<i>M. iliiochantericus medius</i>	<i>M. iliotibialis lateralis</i>	<i>M. flexor digitorum longus</i>
Family Ploceidae							
Subfamily Viduinae							
<i>Vidua paradisaea</i>	2	—	—	+	—	Type 2	ABB
Subfamily Bubalornithinae							
<i>Bubalornis albirostris</i>	2	—	—	+	+	Type 2	ABB
<i>Dinemellia dinemelli</i>	2	—	—	+	+	Type 2	ABB
Subfamily Passerinae							
<i>Plocepasser mahali</i>	1	0.50	small	+	+	Type 1	ABB
<i>Pseudonigrita cabanisi</i>	2	—	medium	+	+	Type 3	ABB
<i>Philetairus socius</i>	1	0.25	medium	+	+	Type 2	ABB
<i>Passer domesticus</i>	1	0.10	large	+	+	Type 2	ABB
<i>Petronia xanthocollis</i>	1	0.10	large	+	+	Type 2	ABB
<i>Montifringilla nivalis</i>	1	0.20	large	+	+	Type 1	ABB
<i>Sporopipes</i> sp.	1	1.00	small	+	+	Type 3	ABB
Subfamily Ploceinae							
<i>Amblyospiza albifrons</i>	2	—	—	+	+	Type 2	ABB
<i>Ploceus ocularis</i>	2	—	medium	+	+	Type 2	ABB
<i>Ploceus nigricollis</i>	2	—	medium	+	+	Type 2	ABB
<i>Ploceus cucullatus</i>	2	—	medium	+	+	Type 2	ABB
<i>Malimbus cassini</i>	2	—	medium	+	+	Type 2	AAA
<i>Quelea quelea</i>	2	—	small	+	+	Type 2	ABB
<i>Foudia madagascariensis</i>	2	—	medium	+	+	Type 2	ABB
<i>Euplectes afer</i>	2	—	—	+	+	Type 2	ABB
<i>Anomalospiza imberbis</i>	2	—	small	+	+	Type 2	ABB
Family Estrildidae							
Tribe Estrildae							
<i>Parmoptila woodhouseii</i>	2	—	—	+	—	Type 2	ABB
<i>Nigrita canicapilla</i>	2	—	small	+	—	Type 3	ABB
<i>Pytilia</i> sp.	2	—	—	+	—	Type 3	ABC
<i>Mandingoa nitidula</i>	2	—	small	+	+	Type 3	ABB
<i>Cryptospiza reichenovii</i>	2	—	—	+	—	Type 3	ABB
<i>Pyrenestes sanguineus</i>	2	—	—	+	—	Type 2	ABB
<i>Pyrenestes ostrinus</i>	2	—	small	+	—	Type 3	ABB
<i>Spermophaga haematina</i>	2	—	—	+	—	Type 3	ABB
<i>Spermophaga ruficapilla</i>	3	—	—	+	—	Type 2	ABB
<i>Clytospiza monteiri</i>	3	—	—	+	—	Type 3	ABB
<i>Hypargos niveoguttatus</i>	1	0.20	—	+	—	Type 3	ABB
<i>Lagonosticta senegala</i>	3	—	—	+	—	Type 3	ABB
<i>Uraeginthus ianthinogaster</i>	2	—	—	+	—	Type 3	ABC
<i>Estrilda paludicola</i>	3	—	small	+	—	Type 3	ABB
<i>Estrilda astrild astrild</i>	3	—	—	+	—	Type 3	ABB
<i>Estrilda astrild angolensis</i>	2	—	—	+	—	Type 3	ABC
<i>Amandava amandava</i>	3	—	—	+	—	Type 3	ABB
<i>Ortygospiza atricollis</i>	2	—	—	+	—	Type 3	ABB
Tribe Poephilae							
<i>Aegintha temporalis</i>	2	—	—	+	+	Type 3	ABB
<i>Emblema guttata</i>	2	—	—	+	+	Type 3	ABB

Table 2.—Continued.

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. ilioprochantericus medius	M. iliotibialis lateralis	M. flexor digitorum longus
<i>Neochmia phaeton</i>	2	—	small	+	+	Type 3	ABB
<i>Poephila guttata</i>	3	—	—	+	+	Type 3	ABB
<i>Poephila acuticauda</i>	2	—	—	+	—	Type 3	ABB
Tribe Lonchurae							
<i>Erythrura trichroa</i>	2	—	small	—	—	Type 3	ABB
<i>Chloebia gouldiae</i>	2	—	—	—	+	Type 3	ABB
<i>Lonchura striata</i>	3	—	—	—	+	Type 3	ABB
<i>Lonchura punctulata</i>	3	—	—	—	+	Type 3	ABB
<i>Padda oryzivora</i>	2	—	—	—	—	Type 2	ABB
<i>Amadina fasciata</i>	2	—	—	+	—	Type 3	ABB

rotic and slightly fleshy origins appear to be the ancestral conditions. The entirely fleshy postacetabular portion represents a derived character state.

M. ILIOTROCHANTERICUS MEDIUS

Structure.—Smallest of the three ilioprochantericus muscles, this band of muscle about 4 mm long and 1 mm wide has a fleshy origin from the ventral edge of the ilium just caudal to the origin of M. ilioprochantericus cranialis. The parallel fibers pass caudoventrally and insert tendinous on the lateral surface of the femur between M. ilioprochantericus caudalis and M. ilioprochantericus cranialis.

Comparison.—This muscle was absent in *Vidua*, in most of the Estrildae examined except *Mandingoa*, and in most of the Lonchurae examined except *Lonchura punctulata*, *L. striata*, and *Chloebia*. In these three species the muscle was very small. It was also absent in *Poephila acuticauda* and present but very reduced in *P. guttata*, *Emblema*, and *Neochmia*.

Discussion.—Designated by the letter "C" in leg-muscle formulas (Hudson, 1937), this muscle is present in many passerine and non-passerine groups (George and Berger, 1966:392). It is universally present in the New World nine-primaried oscines, a group of families that is very close to the Old World finches (Raikow, 1978). By the outgroup comparison its presence in the Old World finches therefore appears to represent an ancestral character state, whereas absence is due to loss and is therefore derived.

M. OBTURATORIUS LATERALIS

Structure.—This muscle has two separate parallel-fibered bellies, pars dorsalis and pars ventralis.

Pars dorsalis arises from the ischium between the caudodorsal border of the obturator foramen and the ventral border of the ilioischiatric fenestra. The belly passes cranio-laterally to a fleshy insertion on the surface of the tendon of insertion of M. obturatorius medialis and the trochanter of the femur. Pars ventralis, the ventral belly, arises fleshy from the cranioventral border of the obturator foramen. The triangular belly passes laterally to insert fleshy on the caudal surface of the femur just distal to the insertion of M. obturatorius medialis. Fibers of pars ventralis may extend dorsally deep to the tendon of M. obturatorius medialis and should not be confused with pars dorsalis.

Comparison.—Pars ventralis is present in all forms studied but pars dorsalis may be absent. When present, pars dorsalis shows considerable variation in size. Raikow (1978) illustrates this variation and defines it as small if the area of origin is not caudal to the obturator foramen, as medium if the origin lies between the obturator foramen and the midpoint of the ilioischiatric fenestra, and as large if the origin lies caudal to the midpoint of the ilioischiatric fenestra. Pars dorsalis was present in all members of the Passerinae studied, and in most of the Ploceinae except *Amblyospiza* and *Euplectes*. It was absent in most of the Estrildidae, *Vidua*, *Bubalornis*, and *Dinemellia* (Table 2).

Discussion.—Pars dorsalis is present in most passerines (George and Berger, 1966; Raikow, 1978), thus by outgroup comparison its absence appears to be a derived state. No accurate statement can be made as to the polarity of the phenocline exhibited by the size of the muscle, as many factors may affect muscle size.

M. GASTROCNEMIUS

Structure.—*M. gastrocnemius* originates by three distinct bellies:

1) *pars externa*—This covers the caudolateral surface of the crus and is intermediate in size between the other two heads. The muscle arises by a short, strong tendon from a tubercle on the caudolateral surface of the femur immediately proximal to the lateral condyle. The tendon of origin is fused with the distal arm of the biceps loop. The belly of *pars externa*, basically unipennate in construction, passes distally and ends in a well-developed tendon that comprises the most lateral portion of the common tendo achillis of the gastrocnemius complex.

2) *pars intermedia*—The smallest of the three heads, *pars intermedia* lies on the medial surface of the crus. The belly of this unipennate muscle is separated from *pars interna* by the tendon of insertion of *M. flexor cruris medialis*. *Pars intermedia* has its origin by a short tendon from a tubercle on the caudoproximal surface of the internal femoral condyle. This origin is shared with the insertion of *M. pubischiofemoralis, pars caudalis*. The short belly of *pars intermedia* ends on an aponeurosis that passes distally between *pars externa* and *pars interna* to form the middle portion of the tendo achillis.

3) *pars interna*—The largest part of this complex, *pars interna* covers most of the medial surface of the crus and consists of two parts. The origin of the cranial head is fleshy from the craniomedial surface of the inner cnemial crest. The caudal head arises from the caudomedial surface of the inner cnemial crest and the head of the tibiotarsus. As noted by Stallcup (1954) this origin is undivided in some species. The belly of *pars interna* extends distally and gives rise to a tendon that joins with the tendons of *pars intermedia* and *pars externa* to form the cranialmost portion of the tendo achillis. This common tendon of insertion passes distally over the tibial cartilage to which it is firmly bound. The insertion is tendinous on the caudal surface of the hypotarsus and along the caudolateral ridge of the tarsometatarsus. The tendon is also bound in and continuous with a fascia which forms a sheath through which other tendons of this region pass.

Comparison.—In *Ploceus* both a cranial and caudal head of origin of *pars interna* are present. When present the cranial head arises, in part, from the inner cnemial crest, whereas a band of muscle (the patellar band) may proceed around the cranial surface of the knee, arising from the patellar ligament.

When present this patellar band overlies the insertion of *M. iliotibialis cranialis*. In this connection three groups may be distinguished (Raikow, 1978). In *Type 1*, the cranial head is present including a patellar band; in *Type 2*, the cranial head is present but lacks a patellar band (as in *Ploceus*); in *Type 3*, the cranial head is absent. These variations are illustrated by Raikow (1978). Forms having *Type 1* vary in the size of the patellar band. This size may be expressed as a percentage of the length of the patellar ligament, which is covered by the muscle origin. For example, a value of 1.00 means that the patellar band arises from the entire extent of the patellar ligament. A value of 0.50 means that it arises from only 50 percent of the patellar ligament (halfway from the rotular crest to the patella). Most of the Passerinae studied had *Type 1*, except *Pseudonigrita*. However, in *Pseudonigrita* a very few fibers may have arisen from the patellar ligament. All members of the Ploceinae, Viduinae, and Bulbournithinae exhibited *Type 2*. Most of the Estrildidae had *Types 1* or *3*. One of the Estrildidae (*Hypargos*) displayed *Type 1* (Table 2).

Discussion.—On the basis of the outgroup comparison with most other birds (George and Berger, 1966:423) and ingroup correlation, *Type 1* is the ancestral state with *Types 2* and *3* being derived from it. *Type 1* occurs mainly in the Passerinae, which with rare exception exhibit no derived character states in other appendicular muscles. *Type 1* also occurs in other groups of birds. *Types 2* and *3* are found in ploceids and estrildids, groups that exhibit other derived character states such as a *Type 2 M. pronator profundus*, loss of the patellar band, and loss of *M. ilirotrochantericus medius* with relatively greater frequency.

M. PLANTARIS

Structure.—This small, triangular muscle lies on the caudomedial side of the crus and has a fleshy origin from the caudomedial surface of the proximal end of the tibiotarsus, just distal to the internal articular surface. The belly is about 6 mm long and tapers to a slender tendon that inserts on the proximomedial corner of the tibial cartilage. The muscle lies deep to *M. gastrocnemius pars intermedia*.

Comparison.—*M. plantaris* was absent in all of the Lonchuridae examined except *Amadina*. In *Euplectes* the belly was reduced to about 1 mm in length (Table 2).

Discussion.—*M. plantaris* is designated by the letter "F" in muscle formulas (Berger, 1959) and

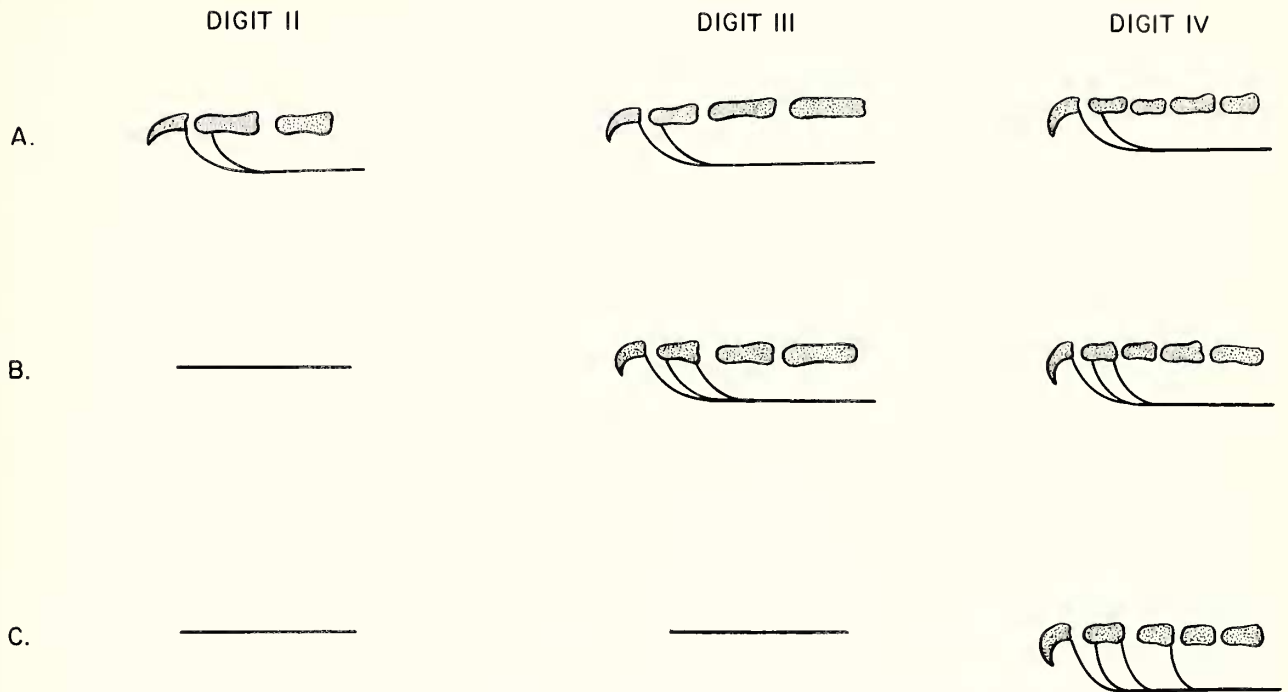


Fig. 4.—Diagram representing variations in the pattern of insertion of *M. flexor digitorum longus*.

was originally thought to be present in all passerines. It occurs in many passerine and non-passerine groups (George and Berger, 1966:442). Its absence therefore represents a loss and is considered to be derived, whereas its presence is an ancestral character state.

M. FLEXOR DIGITORUM LONGUS

Structure.—This large bipennate muscle lies along the caudal surfaces of the tibiotarsus and fibula. There are two separate heads of origin. The lateral head arises fleshy from the caudal surface of the fibula. The medial head arises fleshy from the area between, but distal to, the articular surfaces of the head of the tibiotarsus. These two heads fuse at about the level of insertion of *M. iliofibularis*. The common belly thus formed remains fused to the tibiotarsus and the fibula for about two-thirds of the distance of the crus and shortly thereafter ends in a thick tendon. The tendon of insertion passes through the medial half of the tibial cartilage and then through the craniomedial canal of the hypotarsus. Just proximal to metatarsal I the tendon trifurcates, sending branches to the plantar surface of each of the foretoes. The branch to digit II perforates the tendon of *M. flexor perforans et perforatus*

digitus II and inserts on the proximal end of the ungual phalanx. A single vinculum arises from the deep surface of the tendon and inserts on the distal end of the second phalanx of digit II.

The branch to digit III is the largest of the three branches. It perforates the tendons of *Mm. flexor perforatus digiti III* and *flexor perforans et perforatus digiti III* and inserts on the proximal end of the ungual phalanx. Two small vincula arise from the deep surface of this tendon. The more proximal vinculum inserts in conjunction with the branches of *M. flexor perforans et perforatus digiti III* on the proximal end of the third phalanx of digit III. The distal vinculum inserts on the distal end of the third phalanx.

The branch-tendon to digit IV perforates *M. flexor perforatus digiti IV* and inserts on the proximal end of the ungual phalanx. Two vincula arise from the deep surface of this tendon also. The more proximal vinculum inserts on the proximal end of phalanx IV of digit IV, whereas the distal vinculum inserts on the distal end of the fourth phalanx.

Comparison.—Variation in this muscle centers on the pattern of insertion of the tendons to digits II, III, and IV, the variation involving the number and position of accessory vincula from the tendon

to the phalanges. These variations may be briefly stated by means of a formula (Fig. 4) as used by Raikow (1978).

The formula for *Ploceus cucullatus* is ABB, as it is in all of the forms studied here with four exceptions. In *Pytilia*, *Uraeginthus*, and *Estrilda angolensis* the pattern of insertion is ABC. In *Malimbus* the pattern of insertion is AAA.

Discussion.—The Old World finches exhibit greater uniformity in the arrangement of accessory vincula than the New World nine-primaried oscines (Raikow, 1978). As almost all forms studied here are ABB this character is of little consequence to this study.

M. EXTENSOR HALLUCIS LONGUS

Structure.—This muscle has two distinct parts. The origin of the minute pars proximalis is fleshy from the craniomedial edge of the proximal end of the tarsometatarsus. The slender belly is about 15 mm long, approximately 0.75 mm wide, and ends

in a threadlike tendon of insertion. This tendon passes over metatarsal I and on to the dorsal surface of the hallux. It then passes through two bands of fibroelastic tissue (the automatic extensor ligament), and inserts on dense, fibrous connective tissue immediately proximal to the base of the ungual phalanx. Pars distalis consists of only a few fibers extending fleshy from the distal end of the tarsometatarsus to insert by a short thin tendon onto the tendon of pars proximalis at about the level of the proximal end of phalanx one of the hallux.

Comparison.—In *Bubalornis* and *Dinemellia* additional fibers arise from the craniomedial surface of the tarsometatarsus. These pass medially to insert on the belly of pars proximalis, all along its tendon of insertion, and ultimately to blend in with pars distalis.

Discussion.—Because the accessory fibers of M. extensor hallucis longus occur only in the Bubalornithinae they represent an autapomorphic character state.

DISCUSSION

Sister group relationships may only be determined on the basis of shared derived character states (synapomorphies). All but one of the variations listed in Tables 1 and 2 were useful in determining relationships. The pattern of insertion of M. flexor digitorum longus is presented purely for the sake of describing that muscle completely.

The relationships determined will be presented in the form of a cladogram. Strictly speaking, a cladogram is not a phylogeny, but a diagram of groups clustered by synapomorphies. However, a cladogram may be hypothesized to represent the phylogeny of a group.

A common problem in the construction of a cladogram is character conflict; that is, different characters may indicate different cladistic branching patterns. These character conflicts arise because the complexity of evolutionary processes in closely related groups is not amenable to an overly simplistic view of cladistic procedure. Mayr (1974) has pointed out that cladists often overlook the frequency with which closely related groups independently achieve derived states because of their common genetic background. Thus, parallelism, convergence, and reversals are to be expected especially when dealing with structurally simple vari-

ations within a close-knit group. Therefore, although it may not be possible to identify positively the cause of each inconsistency individually, as a group they are attributable to normal biological causes, and can be accommodated in an overall hypothesis of genealogical relationships. In these situations the convention is to adopt the most parsimonious explanation, although there is no biological basis for assuming that the simplest explanation is also the one most likely to reproduce the true history of the group. It may be best to state that parsimony should be employed not because nature is parsimonious but because only parsimonious hypotheses can be defended without resorting to either authoritarianism or apriorism (Wiley, 1975:236). More recently, Farris (1977) demonstrated that the use of most parsimonious trees in phylogenetic analysis may be justified as a statistical inference method.

I will now discuss the cladogram (Fig. 5), which is similar in format to that of McKenna (1975).

It must first be determined whether or not the Old World finch assemblage is monophyletic. The only unambiguous way to do this would be to demonstrate that the group shares some synapomorphy not found in other birds. Unfortunately, this cannot

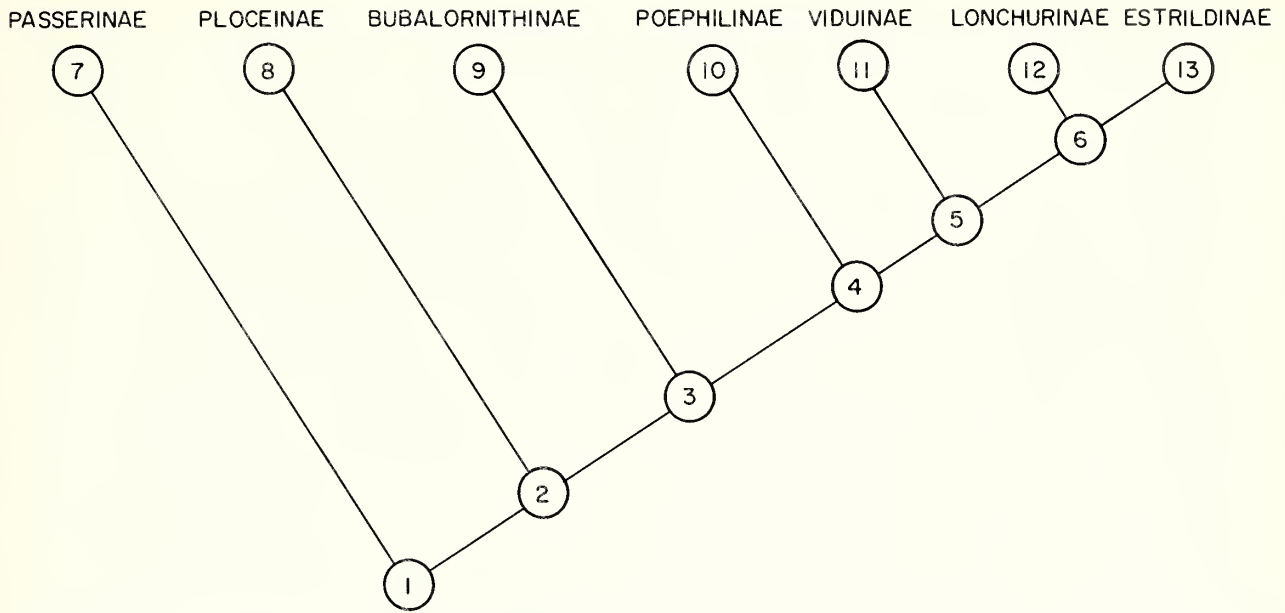


Fig. 5.—A cladogram indicating a hypothesis of phylogenetic relationships in the Ploceidae and Estrildidae. Points 2–13 indicate apomorphic states: (1) noncladistic data supporting hypothesis of monophyly (conical bill and granivory; biochemical evidence; pterylosis); (2) loss of patellar band of *M. gastrocnemius*; (3) loss of *M. obturatorius lateralis pars dorsalis*; (4) presence of mouth markings and loss of *M. coracobrachialis cranialis*; (5) loss of *M. ilioprochantericus medius*; (6) fleshy origin of postacetabular portion of *M. iliotibialis lateralis*; (7) loss of *M. coracobrachialis cranialis*; (8) independent loss of *M. coracobrachialis cranialis*; (9) presence of accessory fibers of *M. extensor hallucis longus pars proximalis*; (10) *M. pronator profundus* Type 2, fleshy origin of postacetabular portion of *M. iliotibialis lateralis*; (11) nest parasitism; (12) elongated belly of *M. tensor propatagialis pars brevis*, loss of *M. plantaris*; (13) *M. pronator profundus* Type 2, loss of *M. latissimus dorsi pars caudalis*.

be done on the basis of present knowledge. No unique character states were found in the limb muscles that would qualify as such characteristics.

The feeding mechanism is another possible source of insight. All of the forms involved have a conical bill used for cracking seeds, which is their principal food. We may hypothesize that this adaptive complex arose once in a common ancestor of the group, and that the Old World finch assemblage thus represents an adaptive radiation paralleling that of the Fringillidae in the New World. Present understanding of the detailed structure of the feeding apparatus does not allow this idea to be tested critically. The idea that the ploceid-estrildid complex is monophyletic has, however, generally been accepted at least implicitly by most workers, because taxonomic problems within this group have mainly centered on generic misplacements and various subgroup divisional difficulties. Delacour (1943:69) and Beecher (1953:303) suggested that the feeding specialization was acquired independently in a number of different families, but neither provided evidence for this opinion. It is clear that this

question is unsettled and that detailed comparative studies of the feeding mechanism in the Ploceidae and Estrildidae are needed. However, on the basis of our present understanding it appears both reasonable and parsimonious to proceed on the tentative assumption that the seed-eating specializations of the ploceid-estrildid complex represent a single adaptive shift rather than a series of convergent developments. Utilizing an unrelated morphological character, pterylosis, Morlion (1966, 1979) found that the ploceids and estrildids shared basic patterns of pterylosis to the extent that separation at the family level was questionable.

Aside from morphological considerations, the most compelling evidence for monophyly is from the biochemical studies of Sibley (1970). Based on electrophoretic studies of egg-white proteins, his principal conclusion was that "the Ploceinae and Estrildinae are related to one another more closely than either is to any other group. Although each seems to be a well-marked, readily defined group they should be placed in the same family" (Sibley, 1970:96). Data of this type cannot be analyzed cla-

distically because the direction of evolutionary changes in molecular structure cannot be determined from electrophoretic patterns. Therefore, these data cannot be used to hypothesize cladistic branching patterns within a group. However, they do demonstrate the close genetic relatedness of the assemblage, which supports the concept that the assemblage constitutes a single radiation, or in other words, that it is monophyletic.

CLUSTER 1

On the basis of the foregoing discussion it is tentatively concluded that the entire assemblage is monophyletic, based on the common seed-eating specialization, pterylosis, and biochemical indications of close genetic affinity.

Most members of the Passerinae (except *Pseudonigrita*) and only members of the Estrildae (except *Hypargos*) possess a Type 1 gastrocnemius. They are postulated to be the most primitive members of this group, and are the sister group of the remainder of this assemblage. They are characterized by a Type 1 gastrocnemius, an obturatorius lateralis pars dorsalis of indeterminate size, a plantaris, an iliotrochantericus medius, an iliotibialis lateralis with an aponeurotic postacetabular origin, no mouth markings, an extensor hallucis longus without accessory fibers, a tensor propatagialis with a long tendon of insertion and no coracobrachialis cranialis.

Poltz and Jacob (1974) analyzed uropygial secretions biochemically in 18 species of passerines and concluded that the Passerinae may be more closely related to the fringillids and emberizine finches than to the ploceids.

CLUSTER 2

The groups linked by character 2 are derived for loss of the patellar band, except *Hypargos* (Estrildae), which is the only form outside of the Passerinae to exhibit a patellar band. Other evidence does not indicate that *Hypargos* has been improperly placed, and this inconsistency could be explained by the secondary reappearance of the patellar band in this form.

CLUSTER 3

Most forms grouped by character 3 are derived for loss of *M. obturatorius lateralis pars dorsalis*. It is also lost in *Euplectes* and *Amblyospiza* of the Ploceinae. *Estrilda paludicola*, *Nigrita*, *Pyrenestes ostrinus*, and *Mandingoa* of the Estrildae, *Eryth-*

rura of the Lonchurae, and *Neochmia* of the Poephilae possess the primitive state. The loss of this muscle in *Euplectes* and *Amblyospiza* probably occurred independently subsequent to the origin of their group.

CLUSTER 4

All of the Poephilae, Viduinae, Lonchurae, and Estrildae have some pattern of mouth markings (character suite 4). Such markings surely represent a derived state as they have never been reported in any other passerine family. Delacour (1943:73) suggested that mouth markings in viduines were acquired by convergence to aid them in their nest parasitism of estrilids. However, Friedmann (1960) argued convincingly for estrilid-viduine affinities. On the basis of plumage, nestling behavior, and reflection globules Friedmann demonstrated that the viduines were closer to the estrilids than to the ploceines and that these markings were acquired from a common ancestor. This position is now strengthened by the fact that the viduines and estrilids are myologically very similar in derived characters. For example, both have lost *M. iliotrochantericus medius*. This suggests that the viduines are a subgroup of the estrilid radiation that has become specialized for nest parasitism of other estrilids, rather than a distantly related group that has converged extensively upon the estrilids. These groups also share another derived state, the loss of *M. coracobrachialis cranialis* (discussed below). They are virtually identical in pterylosis and differ collectively from the Ploceinae (Morlion, 1966, 1979).

CLUSTER 5

Most of the Lonchurae and Estrildae as well as *Vidua* have lost *M. iliotrochantericus medius*, but there are a few exceptions (Table 2). In the Estrildae, it occurs only in *Mandingoa*. Perhaps this genus is misplaced and should be included in the Poephilae in which the muscle occurs with greater regularity. More probably it is a case of parallel loss of the muscle, indicating an underlying genetic tendency in the group. Possibly there are secondary reappearances here also (Raikow et al., 1979). Mayr (1974:80) discusses such cases.

CLUSTER 6

Most of the Estrildae and Lonchurae are derived for a fleshy origin to the postacetabular portion of *M. iliotibialis lateralis*. The exceptions are *Sper-*

mophaga ruficapilla, *Lagonosticta*, *Parmoptila*, *Pyrenestes sanguineus*, *Padda*, and *Aegintha*. The Poephilae also exhibit this condition but for reasons of parsimony are not grouped here. This is discussed below. Only two of the Passerinae (*Plocepasser* and *Montifringilla*) exhibit the ancestral condition of this muscle. Most likely the remaining members of the Passerinae acquired the derived state independently.

AUTAPOMORPHIC CHARACTERS

Characters 7 through 13 are autapomorphic. That is, they are derived character states that are not shared with other groups.

Characters 7 and 8 are both loss of *M. coracobrachialis cranialis*. Separate numbers are given to the same event because the loss of this muscle in one lineage is apparently independent of its loss in the other. Because this muscle is present in many non-passerine birds, its presence in *Bubalornis* and *Dinemellia* presumably is an ancestral condition. This muscle has probably been overlooked in many passerine birds due to lack of adequate staining methods by earlier investigators. When the muscle is not present it is usually represented by a ligamentous band with only a few muscle fibers and imbedded in dense connective tissue as in *Ploceus*. The loss of *M. coracobrachialis cranialis* in the Passerinae, Ploceinae, viduines, and estrildids and the retention of this muscle in the Bubalornithinae represents a case of character conflict. The parsimonious choice, however, is to incorporate the synapomorphies of the Bubalornithinae first, namely the loss of the patellar band and loss of the dorsal head of obturatorius lateralis. Independent loss of a single muscle at several points (4, 7, and 8) then becomes more probable than a single lineage acquiring two derived character states independently, especially because the loss of this muscle appears to be a frequent occurrence in passerines (Raikow, personal communication). An alternative possibility is that this muscle was absent in the common ancestor of the group, and that it reappeared secondarily in the Bubalornithinae. This explanation appears to be less probable than multiple loss, which is a well established and common phenomenon.

Character 9 is the presence of accessory fibers of *M. extensor hallucis longus pars proximalis* in *Bubalornis* and *Dinemellia* only. Such fibers have not been described before and their occurrence here is clearly derived.

Character suite 10 includes two states here con-

sidered autapomorphic, the independent origin of a fleshy postacetabular portion to iliobtibialis lateralis, and a Type II *M. pronator profundus*. Only members of the Estrildae and Poephilae show the latter condition (Table 2) and its occurrence is rather sporadic. Raikow (manuscript) has interpreted this condition as perhaps increasing the functional versatility of the muscle because each belly could act independently of the other. In any event the double belly appears to be just becoming established in these groups, and to have arisen independently in several genera.

Character 11 is nest parasitism. Nest parasitism is also practiced by the ploceine finch *Anomalospiza imberbis* (Roberts, 1917). The viduine finches all have this behavior and are specific parasites of estrildids, whereas *Anomalospiza* parasitizes cisticoline warblers. Although nest parasitism occurs in other groups of birds (Friedmann, 1929), its occurrence within the Old World finches is surely a derived state.

Character suite 12 is elongation of the belly of *M. tensor propatagialis pars brevis* and loss of the plantaris. Both of these derived states occur only among the Lonchuridae. Of all the Lonchuridae examined only *Amadina* retains the plantaris.

Character suite 13 is the presence of a Type II *M. pronator profundus* and the loss of *M. latissimus dorsi pars caudalis*. This latter muscle is one whose pattern of occurrence is also difficult to interpret. In this study the muscle is present in all Ploceinae, Bubalornithinae, Poephilae, Viduinae, and Lonchuridae. It is absent in certain species of Estrildae and also in *Passer*, *Petronia*, and *Montifringilla* of the Passerinae (see Table 1). The muscle may even occur in one species and be absent in another species of the same genus (for example, *Estrilda*). All of this suggests that this muscle may be lost and subsequently regained in an evolving lineage. At the very least the absence of this muscle in estrildines further suggests that they are not closely related to the ploceids.

Although a cladogram is not intended to be a phylogeny *per se*, an ideal cladogram should not present any incompatibilities with other available information about the taxa included. One such source of information is geographic distribution. Among the taxa of the Old World finches, the only groups for which the limb myology could support more than one possible arrangement in the cladogram are the subfamilies of the Estrildidae. Of these, the Viduinae and Estrildinae are endemic to Africa; the

Poephilinae are confined to Australia and New Guinea; and the Lonchurinae are widely distributed, with the genus *Lonchura* found from Africa to Australia but its chief radiation in southeast Asia and the East Indies, one endemic African genus (*Amdina*), two monotypic Australian genera (*Chloebia*, *Aidemosyne*), and one genus only tentatively placed in the Lonchurinae by Mayr (in Mayr et al., 1968:361), *Erythrura*, found from the Philippines through the East Indies, New Guinea, and the Pacific Islands, with a bare foothold in northern Australia.

It seems apparent that, in view of the parasitism of Viduinae on Estrildinae, of their present distribution, and of their close resemblance in many mor-

phological characters, these two subfamilies must have evolved together for some time, and that a cladogram that separated them widely would represent a highly improbable interpretation of the evidence. The common ancestor of all Estrildidae may well have inhabited Africa, where the main radiation of the family has taken place, or else southern Asia. An early invasion of the Australian region radiated into the present Poephilinae, with the lonchurine inhabitants of Australia and vicinity representing a later invasion. Similarly, the lonchurine inhabitants of Africa probably represent a later invasion of a basically East Asian radiation. The cladogram proposed here is compatible with such a distributional history.

CONCLUSIONS AND TAXONOMIC RECOMMENDATIONS

We may now consider the problems posed at the beginning of this study. First of all, should the ploceines and estrildines be classified in one family or two? This question is meaningful mainly from a point of view emphasizing phenetic clustering. Essentially, it asks whether the estrildids are sufficiently different from the remainder of the group so as to be given family rank. They differ in nest construction and mouth markings (Chapin, 1917), in osteology (Sushkin, 1927), and in egg-white proteins (Sibley, 1970). The present study has also demonstrated that they are myologically distinct. I suggest therefore that it would be appropriate for the Estrildidae to be given family rank if one does not feel bound to classify according to the system of Hennig (see Mayr, 1974, for a discussion of cladistic classification).

The above question may also be approached from a cladistic viewpoint. The phylogeny of the group (Fig. 5) shows that the subgroups of the Estrildidae (including the Viduinae) share a common ancestor that is not shared by the others. The estrildid portion of the group is thus holophyletic and warrants some categorical name. However, the remainder of the group (Passerinae, Ploceinae, Bubalornithinae) form a paraphyletic assemblage and cannot be a coordinate sister group of the estrildids. Under strict application of cladistic theory, if one makes the Estrildidae a family then the entire Old World finch assemblage would have to be given higher taxonomic rank. One could also make the entire assemblage a family based on the convention that

the category "family" usually represents a group with a readily discernible adaptive niche—in this case the seed-eating specialization. Basically, these are matters of individual preference depending on a worker's systematic philosophy.

The exact position of *Passer* has been a problem for some time. It has never been conclusively demonstrated whether the genus is more closely related to the ploceines, estrildines, fringillids, or to another group. There is little doubt that *Passer* is a unique genus among the Old World finches in terms of nest construction and geographic distribution. Though no conclusive statement can be made as to the exact status of *Passer*, it appears as though it is myologically most similar to other members of the Passerinae. However, the Passerinae are seen to be the most primitive members of this group (Fig. 5) and additional work could reveal that certain genera may be more closely related to the fringillids, as suggested by Poltz and Jacob (1974) and Sibley (1970) for *Passer*.

Sibley (1970) recommended that a family Passeridae be recognized for *Passer* and stated that the relationships of *Montifringilla* were probably not with *Passer*. Clench (1970) found that in pterylosis *Passer* was similar to *Pseudonigrita* and *Plocepasser* but differed significantly from *Sporopipes*. The present study shows that the Passerinae are characterized by a certain myological uniformity. The above genera, as well as others, all possess a pectoral band and retain the dorsal head of obturatorius lateralis (Table 2). Although some variation oc-

curs in the origin of iliobtibialis lateralis, the members of the Passerinae are myologically more similar to each other than to any group investigated here. However, these similarities are mostly ancestral character states and thus relatively weak indicators of relationship. *Passer* and *Montifringilla* are myologically unique members of the Passerinae in that they both share the derived condition of *M. deltoideus minor* (Table 1). These two genera, along with *Petronia*, also differ from other Passerinae in the derived absence of *M. latissimus dorsi pars caudalis*. It appears then that these three genera are probably closely related. Bock and Morony (1978) reached a similar conclusion based on a study of the tongue skeleton.

Certain authors (Sushkin, 1927; Collias and Collias, 1964) have recognized such subfamilies as the Plocepasserinae and the Sporopipinae. Although there may be an adequate osteological and behavioral basis for such groupings, there is no myological reason for the recognition of those groups. It is recommended that the subfamily Passerinae be retained and that the genera listed under that section in Table 1 be included in that subfamily.

The relationships of the Widow Birds (*Vidua*) have also been debated. On the basis of egg-white proteins, *Vidua* most closely resembled *Passer* (Sibley, 1970). Historically, however, the ploceines, euplectines, and estrildines have been considered as possible relatives. On the basis of reflection globules in the mouth, nestling behavior, plumage, and pterylosis, Friedmann (1960) and Morlion (1966, 1979) decided that the viduines were most closely related to the estrildines. The present study has demonstrated that in derived characters the viduines are also myologically more similar to the estrildids than to the ploceids. If separate families are to be recognized, then the subfamily Viduinae should be included within the Estrildidae and not within the Ploceidae. This is in marked contrast with what has stood as the "preferred" classification for this assemblage (Sushkin, 1927). Also within the "Check-list of Birds of the World" (Mayr et al., 1968) the Viduinae are listed under the Ploceidae. It is further recommended (if separate families are recognized) that the subgroups of the Estrildidae (Mayr et al., 1968, based on the tribes of Delacour, 1943, but given the termination -ae instead of the proper tribal termination -ini) be raised

to subfamily status because this is the first subdivision of the family category, whereas the tribal category is normally used as a subdivision of the subfamily category. Thus, the Estrildae would become the Estrildinae, the Poephilae would become the Poephilinae, and the Lonchurinae would become the Lonchurinae.

On the basis of comparative myology it is also possible to make some general conclusions as to the closest relatives of certain other genera. It is generally agreed that *Dinemellia* is the closest relative of *Bubalornis*, and that relationship is supported by the present study. Sushkin (1927) believed that *Bubalornis* was more primitive than *Dinemellia*, and was considered to be the most primitive of all ploceids. However, only *Bubalornis* possesses an *M. expansor secundariorum* that inserts on four secondaries. This, and the presence of a copulatory organ, are derived states and suggest that *Bubalornis* is derived relative to *Dinemellia*. It has been demonstrated then that *Bubalornis* is derived in a number of myological, osteological, and morphological traits and does not represent the most primitive of ploceids. Therefore if there are sturnid affinities to the Ploceidae (Bartlett, 1889), they are not through *Bubalornis*. Data from egg white proteins did not support a sturnid-*Bubalornis* affinity (Sibley, 1970).

Philetairus, *Sporopipes*, and *Plocepasser* are myologically good members of the Passerinae but appear to be more closely related to each other than to *Passer* and the other members of the subfamily.

Do the Old World finches then represent a monophyletic group? The myological evidence as well as evidence from other disciplines discussed above suggests that this group as a whole is probably monophyletic.

On the basis of this study the following classification is proposed:

Family	Ploceidae
Subfamilies	Passerinae
	Ploceinae
	Bubalornithinae
Family	Estrildidae
Subfamilies	Poephilinae
	Viduinae
	Lonchurinae
	Estrildinae

ACKNOWLEDGMENTS

This study was completed as partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Pittsburgh. I would like to thank Dr. Robert J. Raikow for his assistance throughout this project. Without his encouragement and advice this work could not have been completed. I am also indebted to the members of my committee: Dr. Kenneth C. Parkes, Dr. Mary H. Clench, Dr. William P. Coffman, Dr. Michael Mares, and Dr. Jeffrey Schwartz. I am grateful to the following for providing the specimens upon which this study is based: Carnegie Museum of Natural History, Dr. Mary H.

Clench; National Museum of Natural History, Dr. Storrs L. Olson; Peabody Museum of Natural History, Yale University, Dr. Charles G. Sibley; American Museum of Natural History, Dr. Walter J. Bock; Museum of Vertebrate Zoology, University of California, Berkeley, Dr. Ned K. Johnson; Occidental College, Dr. Luis F. Baptista; British Museum (Natural History), Dr. Philip Burton.

Portions of this study were supported by NSF Grant No. BMS 74 18079 to Dr. Robert J. Raikow.

LITERATURE CITED

- BARTLETT, E. 1889. A monograph of the Weaverbirds, Ploceidae, and Arboreal and Terrestrial Finches, Fringillidae. London, 193 pp.
- BEECHER, W. J. 1953. A phylogeny of the oscines. *Auk*, 70:270-333.
- BERGER, A. J. 1959. Leg-muscle formulae and systematics. *Wilson Bull.*, 71:93-94.
- . 1968. Appendicular myology of Kirtland's Warbler. *Auk*, 85:594-616.
- BOCK, W. J. 1960. The palatine process of the premaxilla in the Passeres. *Bull. Mus. Comp. Zool.*, 122:361-488.
- BOCK, W. J., AND J. J. MORONY, JR. 1978. Relationships of the passerine finches (Passeriformes:Passeridae). *Bonn Zool. Beitr.*, 29:122-147.
- BOCK, W. J., AND R. SHEAR. 1972. A staining method for gross dissection of vertebrate muscle. *Anat. Anz.*, 130:222-227.
- CHAPIN, J. P. 1917. The classification of Weaver-Birds. *Bull. Amer. Mus. Nat. Hist.*, 37:243-280.
- CLENCH, M. H. 1970. Variability in body pterylosis, with special reference to the genus *Passer*. *Auk*, 87:650-689.
- COLLIAS, N. E., AND E. C. COLLIAS. 1964. Evolution of nest-building in the Weaverbirds (Ploceidae). *Univ. California Publ. Zool.*, 73:1-162.
- DELACOUR, J. 1943. A revision of the subfamily Estrildinae of the family Ploceidae. *Zoologica*, 28:69-86.
- DELACOUR, J., AND F. EDMOND-BLANC. 1933-34. *Monographie des veuves (revision des genres Euplectes et Vidua.) L'Ois.*, 3:519-562, 687-726, 4:52-110.
- FARRIS, J. S. 1977. Phylogenetic analysis under Dollo's Law. *Syst. Zool.*, 26:77-88.
- FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois, 421 pp.
- . 1960. The parasitic Weaverbirds. *Bull. U.S. Nat. Mus.*, 223:viii + 1-196.
- GEORGE, J. C., AND A. J. BERGER. 1966. *Avian myology*. Academic Press, New York and London, xii + 500 pp.
- HENNIG, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana, 263 pp.
- HUDSON, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. *Amer. Midland Nat.*, 18:1-108.
- KLUGE, A. G. 1971. Concepts and principles of morphologic and functional studies. Pp. 3-51, *in* Chordate structure and function (A. J. Waterman, ed.). Macmillan Company, New York, 628 pp.
- MASLIN, T. P. 1952. Morphological criteria of phyletic relationships. *Syst. Zool.*, 1:49-70.
- MAYR, E. 1955. Comments on some recent studies of song bird phylogeny. *Wilson Bull.*, 67:33-34.
- . 1974. Cladistic analysis or cladistic classification? *Z. Zool. Syst. Evol.-forsch.*, 12:94-128.
- MAYR, E., R. A. PAYNTER, JR., AND M. A. TRAYLOR. 1968. Family Estrildidae. Pp. 306-389, *in* Check-list of birds of the World (R. A. Paynter, ed.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 14:x + 1-433.
- MCKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21-46, *in* Phylogeny of the Primates (W. P. Luckett and F. S. Szalay, eds.), Plenum Publ. Corp., New York, xiv + 483 pp.
- MOREAU, R. E., AND J. C. GREENWAY, JR. 1962. Family Ploceidae. Pp. 3-74, *in* Check-list of birds of the World (E. Mayr and J. C. Greenway, Jr., eds.), *Mus. Comp. Zool.*, Cambridge, Massachusetts, 15:x + 1-315.
- MORLION, M. 1966. *Vergelijkende studie van de pterylosis in enkele Afrikaanse genera van de Ploceidae*. Unpublished Ph.D. thesis, Rijksuniversiteit Gent, Belgium, 399 pp.
- . 1979. Pterylosis as a secondary criterion in the taxonomy of the African Ploceidae and Estrildidae. Ostrich, in press.
- POLTZ, J., AND J. JACOB. 1974. Burzeldrusensekrete bei Ammern (Emberizidae), Finken (Fringillidae) and Webern (Ploceidae). *J. Ornithol.*, 115:119-127.
- RAIKOW, R. J. 1976. Pelvic appendage myology of the Hawaiian honeycreepers (Drepanidae). *Auk*, 93:774-792.
- . 1977. Pectoral appendage myology of the Hawaiian honeycreepers (Drepanidae). *Auk*, 94:331-342.
- . 1978. The appendicular myology and relationships of the New World nine-primaried oscines (Aves:Passeriformes). *Bull. Carnegie Mus. Nat. Hist.*, 7:1-43.
- RAIKOW, R. J., S. R. BORECKY, AND S. L. BERMAN. 1979. The evolutionary reestablishment of a lost ancestral muscle in the Bowerbird assemblage. *Condor*, in press.

- REICHENOW, A. 1914. *Die Vogel: Handbuch der Systematischen Ornithologie*. Vol. II. Verlag von Ferdinand Enke, Stuttgart, 628 pp.
- ROBERTS, A. 1917. Parasitism amongst finches. *Ann. Transvaal Mus.*, 5:259-262.
- . 1947. Reviews and criticisms of nomenclatural changes. *Ostrich*, 18:59-85.
- ROSS, H. H. 1974. *Biological systematics*. Addison-Wesley, Reading, Massachusetts, 345 pp.
- SHELLEY, G. E. 1905. *The birds of Africa*. R. H. Porter, London, 6(part 1):v + 1-511.
- SIBLEY, C. G. 1970. A comparative study of the egg-white proteins of passerine birds. *Bull. Peabody Mus. Nat. Hist., Yale Univ.*, 32:1-131.
- STALLCUP, W. B. 1954. Myology and serology of the avian family Fringillidae, a taxonomic study. *Univ. Kansas Publ., Mus. Nat. Hist.*, 8:157-211.
- STEINER, H. 1954. Das Brutverhalten der Prachtfinken, Spermestidae, als Ausdruck ihres selbständigen Familiencharakters. *Eleventh Int. Cong. Orn. Basel*, pp. 350-355.
- SUSHKIN, P. P. 1927. On the anatomy and classification of the weaverbirds. *Bull. Amer. Mus. Nat. Hist.*, 57:1-32.
- TORDOFF, H. B. 1954. A systematic study of the avian family Fringillidae based on the structure of the skull. *Misc. Publ. Mus. Zool., Univ. Michigan*, 81:1-41.
- TRAYLOR, M. A. 1968. Family Ploceidae, subfamily Viduinae. Pp. 390-397, *in* *Check-list of birds of the World* (R. A. Paynter, ed.), *Mus. Comp. Zool., Cambridge, Massachusetts*, 14:x + 1-433.
- WILEY, E. O. 1975. Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. *Syst. Zool.*, 24:233-243.
- WOLTERS, H. E. 1949. Beiträge Zur Gattungssystematik der Finkvogel. *Beit. Gattungs. Vogel*, 1:3-17.